

Heterogeneity in patterns of survival of the invasive species *Ipomoea carnea* in urban habitats along the Egyptian Nile Delta

Reham F. El-Barougy^{1,2}, Marc W. Cadotte^{1,3,4}, Abdel-Hameed A. Khedr²,
Reham M. Nada², J. Scott MacIvor³

1 Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St. Toronto, Ontario, Canada **2** Department of Botany, Faculty of Science, Damietta University, Egypt **3** Department of Biological Sciences, University of Toronto Scarborough, 1265 Military Trail, Toronto, ON, Canada **4** State Key Laboratory of Biocontrol, Key Laboratory of Biodiversity Dynamics and Conservation of Guangdong, Higher Education Institutes, College of Ecology and Evolution, Sun Yat-sen University, Guangzhou, PR China

Corresponding author: Reham F. El-Barougy (reham.el.barougy@mail.utoronto.ca)

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Abstract

Plant traits are critical for understanding invasion success of introduced species, yet attempts to identify universal traits that explain invasion success and impact have been unsuccessful because environment-trait-fitness relationships are complex, potentially context dependent, and variation in traits is often unaccounted for. As introduced species encounter novel environments, their traits and trait variability can determine their ability to grow and reproduce, yet invasion biologists do not often have an understanding of how novel environments might shape traits. To uncover which combination of traits are most effective for predicting invasion success, we studied three different urban habitat types along the Nile Delta in Egypt invaded by the Pink Morning Glory, *Ipomoea carnea* Jacq. (Family: Convolvulaceae). Over two years, we measured ten plant traits at monthly intervals along an invasion gradient in each habitat. No single trait sufficiently explained survival probability and that traits linked to invasion success were better predicted by the characteristics of the invaded habitat. While the measured traits did influence survival of *I. carnea*, the importance of specific traits was contingent on the local environment, meaning that local trait-environment interactions need to be understood in order to predict invasion.

Keywords

Invasion success, Exotic species, Survival probability, Morning Glory, Disturbed habitat

Introduction

Biological invasion is a significant threat to biodiversity and often leads to habitat degradation (Elton 1958, Genovesi and Monaco 2013, Qureshi et al. 2014). There is a great need for efficient tools to predict invasion success and impact on native ecosystems (Funk et al. 2008). Yet, the relative importance of particular life history and functional traits for invasion success and impact is strongly context-dependent and likely to change across environments (Dawson et al. 2009). In cases of significant impact by invasive plants, estimating ‘invasiveness’ using plant traits that predict plant survival could be used to determine invasion resistance of native plant communities (Ortega and Pearson 2005, Radosevich et al. 2007, Colautti et al. 2014). This is particularly important to understand in urban habitats where urbanization can favor non-native species (McKinney 2006). Urbanization reduces the competitiveness of established vegetation (Wilson and Tilman 1995) and increases the availability of resources (Johnstone 1986, McConnaughay and Bazzaz 1991), which can be exploited by non-native species, further influencing their invasiveness.

At a more basic level, we often lack a basic understanding of how size and life history traits contribute to the successful growth and reproduction of most species and especially non-native species. The attributes that are associated with successful species is undoubtedly correlated with local environmental conditions (Laughlin et al. 2012, Laughlin 2014). For example, Laughlin and colleagues (2012) show how models that match trait values to local climate predict species abundances. Such a relationship between traits and the environment are useful to explain presence/absence or abundance patterns, but little work has been done to see if intraspecific trait variation can explain difference in growth, reproduction, and survival. Further, it is unclear how changes in size-based traits through the growing season and in different environments influence success. What is lacking in our current knowledge is how specific traits or suites of traits influence species performance in different habitats.

A number of studies have shown that invasion success can be linked to specific traits and the degree to which they promote survival in novel environments. These include for example, traits linked with reproduction and dispersal, leaf traits that are believed to reflect competitive strategies, overall resource allocation into growth, and seedling growth patterns (Usher 1988, Pattison et al. 1998, Reichard and Hamilton 1997, Kolar and Lodge 2001, Richardson and Rejmánek 2004, Hamilton et al. 2005, Rejmánek et al. 2005). Leaf traits linked to species success are associated with their ability to capture resources, particularly in environments that are resource limited (Funk and Vitousek 2007). For invasive plants, leaf carbon fixation strategies that improve productivity are closely linked to success in introduced habitats (Wright et al. 2004, Westoby and Wright 2006).

While the search for the attributes that influence species performance and especially invasion would undoubtedly lead to advancing general theory, it is often underappreciated just how sensitive trait-performance relationships can be to local environmental conditions. The appreciation of the importance of intraspecific trait variation

has greatly increased in community ecology (Albert et al. 2012, Violle et al. 2012), but our understanding of how specific traits, and their variation, influence plant species growing in different habitats is lacking.

This study investigates the aboveground and belowground plant attributes, and especially those that reflect resource allocation, that influence the survivorship of the invasive pink morning glory, *Ipomoea carnea* Jaq. (Family: Convolvulaceae), in three unique urbanized habitats that it invades in the Nile Delta region in Egypt. *Ipomoea carnea* is an annual vine that is native to Central and South America, but occurs worldwide in many habitats, including the Nile Delta where it is invasive (Eid 2002, Shaltout et al. 2010). This species reproduces vegetatively and the reproductive vegetative unit is called ramet (an individual stalk from one individual plant) which originates from a semi-underground organ, the caudex. This type of reproduction is very common and considered as a proxy for the successful invasion of *I. carnea*, additionally it reproduces by seeds and the reproductive unit is called genet which is rarely occurred due to the harsher conditions that required for seed germination. To explore population growth rates of the invasive plant, and how they respond to environmental variation, we used density-independent matrix models (Engelen and Santos 2009, Griffith 2010) to evaluate the survivorship of *I. carnea* in three introduced habitats (Eid 2002, Jerde and Lewis 2007, Bates et al. 2013). We tested three hypotheses 1) there are specific plant traits that predict the survival probability of *I. carnea* along an urbanization gradient 2) there is variation in the survival probability in different urban habitat types which is highest in canal banks habitat followed by roadsides and waste lands, representing an urban gradient, and that 3) leaf traits are the best indicators of the successful invasion of *I. carnea*. Our findings provide valuable information on specific traits that determine invader survival in different novel urban habitat types for a species that is prevalent worldwide.

Methods

Sites

The study area is bound by the main tributaries of the Nile Delta in Egypt, from the Rosetta branch at the west to the Damietta Governorate at the east, the Mediterranean Sea to the north and the Menoufia Governorate to the South. The area of the Nile Delta is about 22,000km² and it comprises about 63% of Egypt's productive agricultural area (Abu Al-Izz 1971).

Nine permanent stands in Damietta Governorate were established in each of three different urban habitats where the invasive *I. carnea* occurred: wastelands, roadsides (both with dry-sandy soil) and canal banks (with clay-organic soil) (Shaltout et al. 2010). In each stand, a map was drawn indicating the spatial distribution of above ground vegetative units (ramets) of *I. carnea*. Mean surviving and dead ramets in each stand was recorded monthly.

Plant trait sampling

Ten randomly distributed quadrats (1×1 m) were laid down in each stand. The number of *I. carnea* ramets in each quadrat was counted and used to estimate *I. carnea* density per stand (ramets/ m^2). Ten ramets (1 per m^2 plot) were randomly selected and marked using flagging tape to monitor the monthly variation in each of the plant traits. The height from the ground (cm), average diameter (cm), leaf area (cm^2), number of flowering ramets, number of non-flowering ramets, number of leaves, flowers and fruits of the canopy for each permanent marked ramet were estimated monthly.

Three randomly selected ramets were harvested from each stand and their roots, stems and leaves were separated and weighted to determine their fresh weights. The roots, stems and leaves were oven dried at 60°C for three days to determine the dry weight. Mean fresh and dry weights of the roots, stems and leaves of the ramets of each habitat were determined (gm ramet^{-1}) and multiplied by the number of ramets (m^{-2}) in each stand to give their standing crop (gm^{-2}) in each habitat (Shaltout and Ayyad 1988, Al-Sodany et al. 2009).

Soil analysis

In each stand, a composite soil sample was collected from beneath invaded and non-invaded canopies from each habitat, each 50 cm deep. These were air dried and passed through a 2 mm sieve to separate gravel and debris. Soil water extracts at 1:5 were prepared for the determination of soil reaction (pH) using a Benchtop pH Meter (Mettler-Toledo).

Statistical analysis

Generalized-multivariable modelling

There were 14 different variables used in generalized multivariable modelling (Table 1). In this analysis, the binomial response variable with two-column was represented by the total observed number of surviving ramets (first column) and dead ramets (second column), while the explanatory variables were represented by plant traits, sampling time and soil (pH) for invaded and non-invaded canopies in the three different urban habitats. We aimed to identify the most parsimonious models that explained which explanatory variables were best for predicting this binomial response variable. To remove potential explanatory variables (predictors), we first constructed a series of models with each of the variables, then we compared the explanatory ability of these models using Akaike's information criterion weights which can be used to interpret which model was the best fit to an observed dataset, among a set of candidate models (Johnson and Omland 2004). We used a chi-square test to test for significance of the model's goodness-of-fit. The best

Table 1. List of measured variables from which the average values were taken from 10 plants per stand in each of the three urban habitats (Canal banks, Wastelands and Roadsides).

Variable	Units	code
Total surviving and dead ramets	-	y
Sampling month	-	M
Leaf area		LA
Diameter	cm	D
Height	cm	H
Number of all leaves	-	NL
Leaf biomass	gm/M ²	LB
Number of flowering ramets	-	Flr
Number of non-flowering ramets	-	NFlr
Number of flowers	-	Fl
Shoot biomass	gm/M ²	SB
Root biomass	gm/M ²	RB
Soil pH under canopy (invaded areas)	-	PhU
Soil pH outside canopy (non-invaded areas)	-	PhO

models were filtered according to 1) lower values of AIC, 2) higher values of model probability (AW), 3) higher p values of chi-square test ($p > 0.05$). We checked diagnostic plots (e.g. residual versus fitted plots) for potential outliers and data trends. We were not only interested in the best single variable explaining the rate of survival probability, but also combining all plant traits in multi-variable models (see Suppl. material 1).

For each urban habitat, we assessed the observed survival probability based on the ratio between the observed number of surviving ramets and total ramets (including surviving and dead ramets), while the fitted survival probability was assessed from each multivariable model as fitted values. We tested the difference between the observed and fitted survival probability values for all multivariable models to confirm that the difference between observed and fitted values from the best model was very low. Further, for each modelled trait, we assessed which trait values tended to have higher or lower survival probabilities. All analyses were completed using R v.3.2.2 (RStudio Team 2015).

Odds ratio (OR)

We modelled the probabilities of survival as a function of the plant traits and environmental variables in different habitats and to do this we used odds ratio to predict the upper and lower limit of the ratio of the probability of success (survival) and the probability of failure (death) for each modelled variable. Odds ratios were also used to test for possible associations between different environmental variables. If the OR is equal to 1, there is no association. If the OR is (> 1 and < 1), then there is a possible statistical association between them (Morris et al. 1988, McHugh 2009, Szumilas 2010). The odds ratios were computed in R using functions *confint* and *exp* in the MASS package.

Results

There was a highly significant effect of habitat on survival probability of *I. carnea* with lower survival probability in wastelands and roadsides compared to canal banks which showed a remarkably highly survival probability. For adult ramet mortality, wasteland and roadside had the highest, while canal banks had the lowest (Fig. 1a).

Generalized Multivariable modelling

Comparing the mean plant trait values and abiotic variables in different habitats, forty generalized linear models were constructed (Suppl. material 1). The most parsimonious model explaining the binomial response variable (the total surviving and dead ramets) in *I. carnea* in the canal banks site included sampling time (month), number of non-flowering ramets, root biomass, number of flowers, number of flowering ramets and leaf area ($AW = 0.606$, $AIC = 102.3$). For wastelands, the best model ($AW = 0.756$, $AIC = 189.41$) included leaf biomass, root biomass, stem diameter, number of leaves

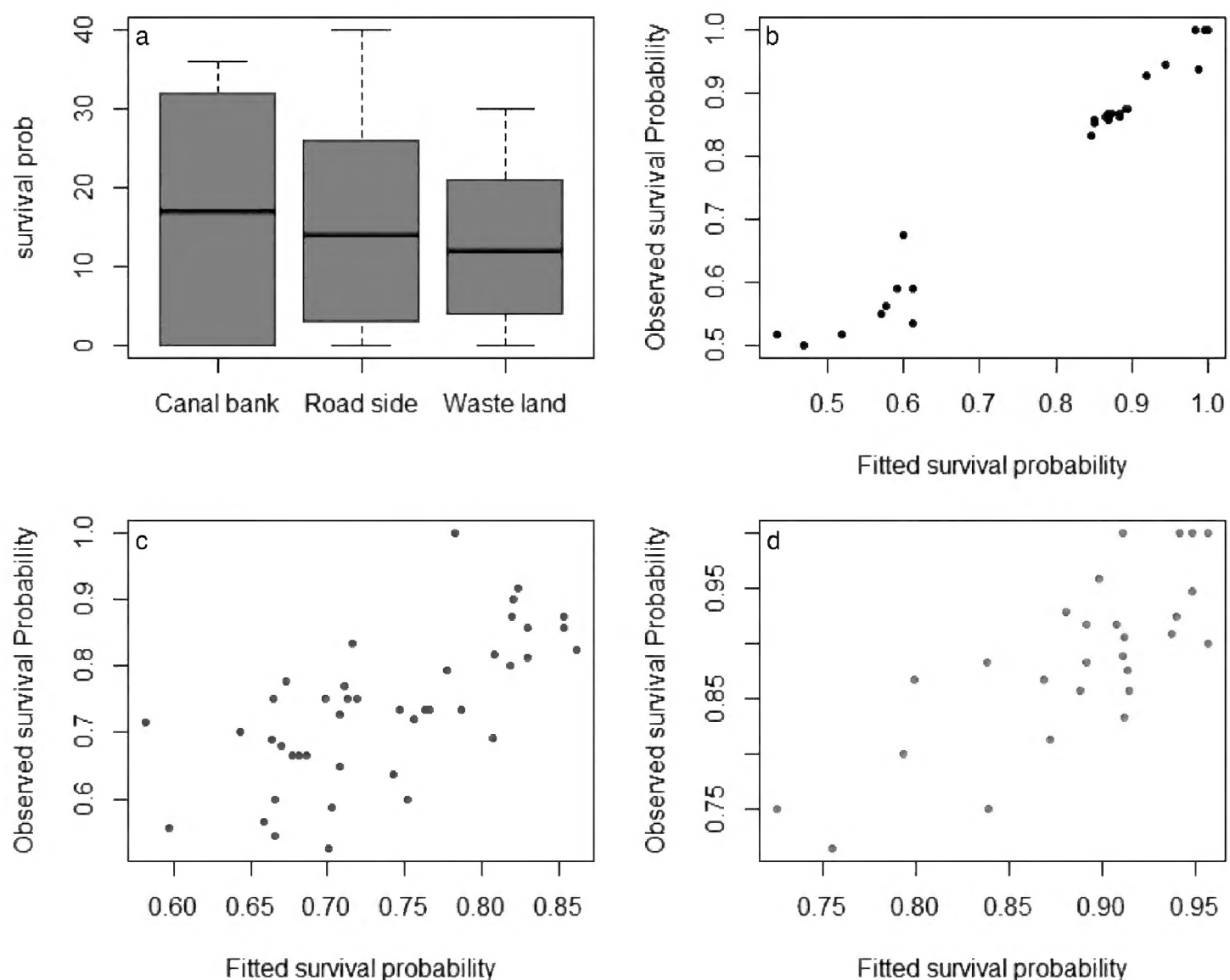


Figure 1. a Comparison between the mean of observed survival probability at habitat level b–d the relationship between fitted survival probabilities from the three top models and survival probabilities from the actual observed data in canal banks, roadsides and wastelands respectively.

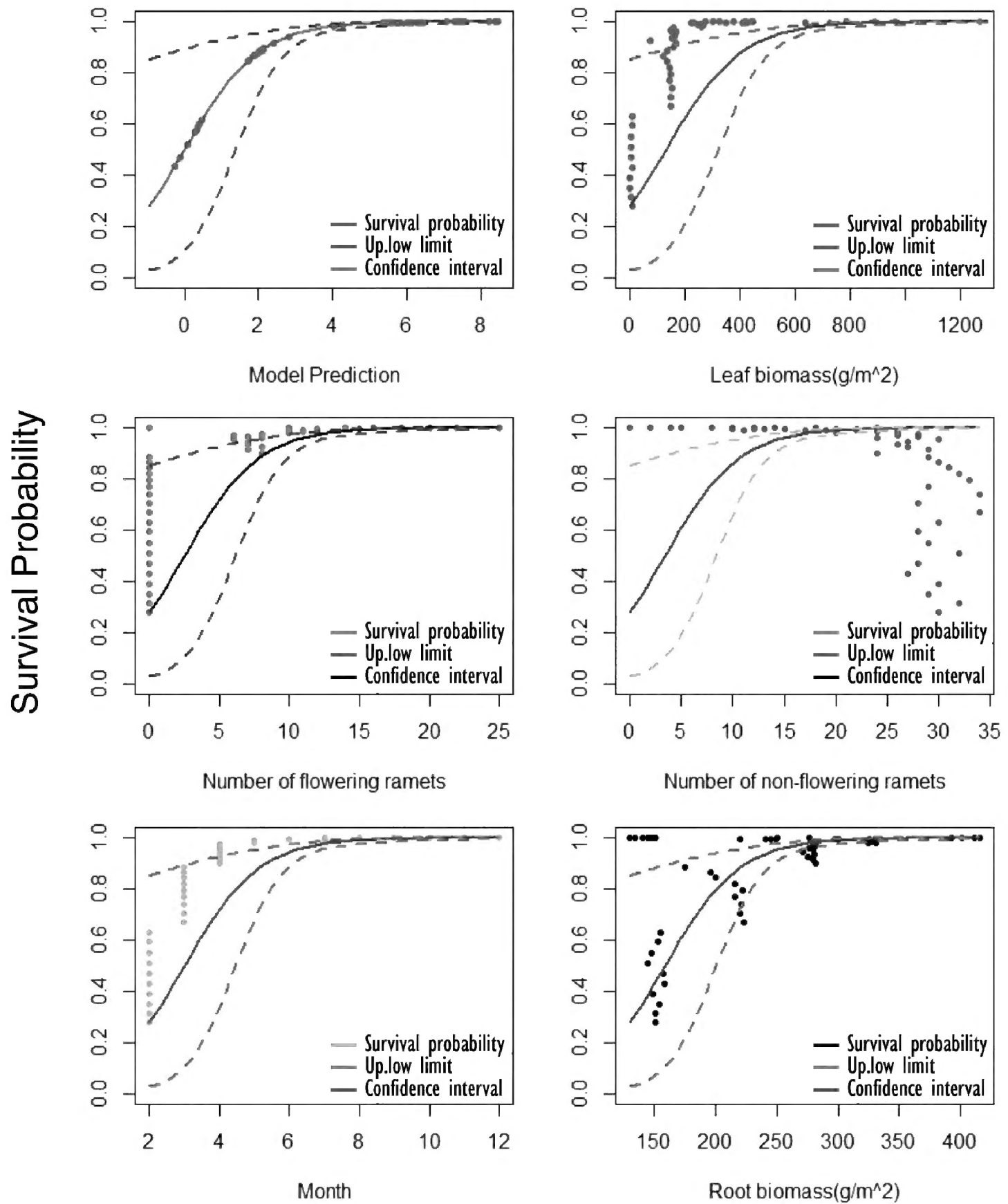


Figure 2. The relationship between survival probability and predictors from the top model for Canal bank habitat.

and soil PH for invaded areas. For roadsides, the best model ($AW = 0.423$, $AIC = 111.1$) included month, stem diameter, flowering ramets, non-flowering ramets and soil pH of invaded areas. These three top models revealed 97.5%, 42.9%, and 50.8% of the deviance explained in canal banks, wastelands and roadsides, respectively (Suppl. material 1).

For the abiotic variables, there was a positive significant interaction between the binomial response variable and sampling time in canal bank, while this interaction

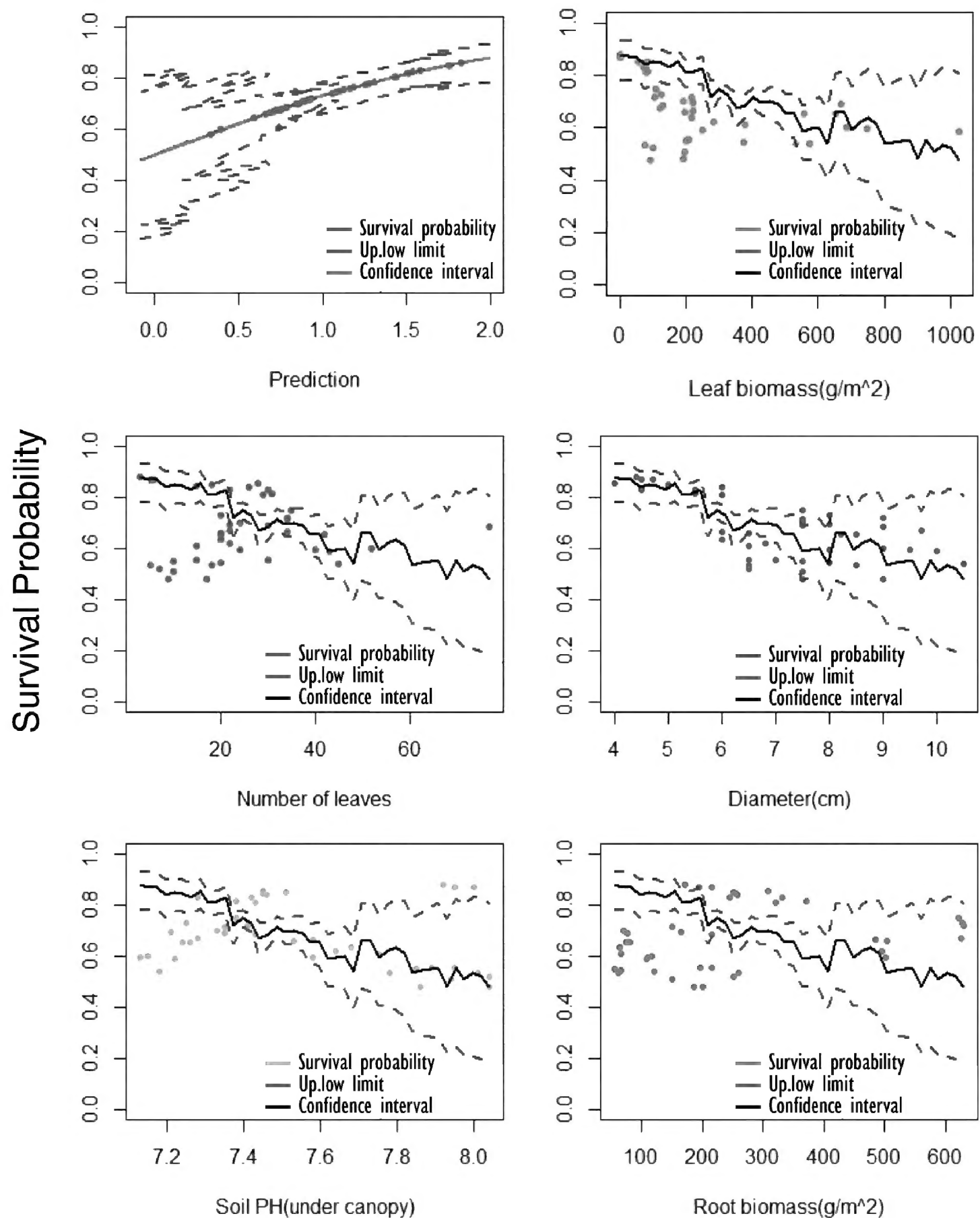


Figure 3. The relationship between survival probability and predictors from the top model for wasteland habitat.

showed a negative significant effect in road side habitats. Additionally, being in soil with high pH (>7) values resulted in lower *I. carnea* survival in wasteland habitat (Table 2).

All of the *I. carnea* biomass traits differed significantly between habitats. Higher values of leaf biomass had a strongly significant negative effect on the survival rate in canal bank and wasteland. Additionally, higher root biomass decreased survival rate in

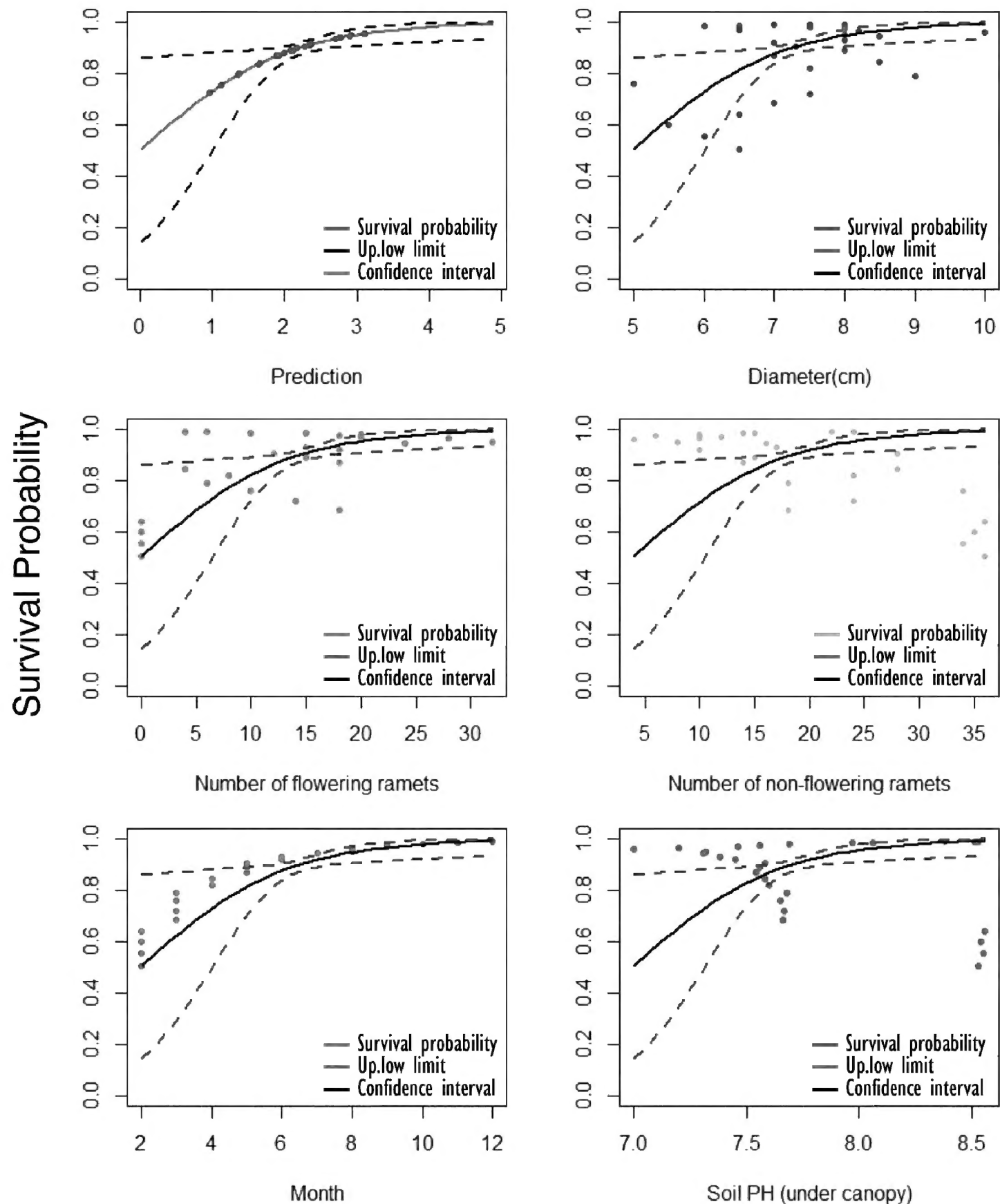


Figure 4. The relationship between survival probability and predictors from the top model for Roadside habitat.

wasteland but increased survival in canal bank. Other traits that significantly increased survival probability included the number of leaves in wasteland habitat, higher values of flowering ramets and non-flowering ramets in road sides, and the number of flowers in canal banks. Although declining stem diameter led to a significant reduction in survival rate in wasteland habitats, smaller stems were positively correlated with survival rate in roadside habitats (Table 2).

Table 2. Comparison of the top multivariable models from the stratified generalized linear models. The confidence interval (CI) with upper (U) and lower limit (L) and odds ratios (OR) for the modelled coefficients in the three habitats: canal banks (CB), roadsides (RS), waste lands (WL). (-) represents a variable that is excluded in the given top model.

Variables	Coefficients			CI (U,L)			Odds ratio (OR)			P-value		
	CB	WL	RS	CB	WL	RS	CB	WL	RS	CB	WL	RS
Month	0.79	-	-0.145	0.577, 1.025	-	-0.24, -0.05	2.2	-	0.86	0.00	-	0.003
Leaf biomass	-0.03	-0.001	-	-0.032, -0.018	-0.002, -2.9×10 ⁻⁴	-	0.97	0.99	-	0.00	0.02	-
# Flowering ramets	0.46	-	0.13	0.276, 0.730	-	0.05, 0.21	1.58	-	1.13	0.00	-	0.000
# Flowers	0.13	-	-	0.055, 0.190	-	-	1.14	-	-	0.00	-	-
# Non-flowering ramets	0.09	-	0.05	-3.2×10 ⁻⁴ , 0.200	-	0.001, 0.11	1.09	-	1.05	0.05	-	0.05
Root biomass	0.02	-0.001	-	-8.5×10 ⁻⁵ , 0.030	-0.002, -1.7×10 ⁻⁶	-	1.01	0.99	-	0.02	0.05	-
Diameter	-	-0.13	0.28	-	-0.25, -1.25×10 ⁻²	0.024, 0.54	-	0.87	1.32	-	0.03	0.03
Number of leaves	-	0.013	-	-	-0.002, 2.8×10 ⁻²	-	-	1.01	-	-	0.10	-
Soil PH (under canopy)	-	-0.79	0.95	-	-1.52, -7.3×10 ²	-0.24, 2.12	-	0.45	2.6	-	0.03	0.11

Furthermore, when we tested the difference between the observed survival probability from actual data and fitted survival probability from the three top models in different habitats, we found that the difference was very low compared to other models (Fig. 1b–d).

Odds ratio (OR)

The odds ratio and confidence interval for modelled variables were interpreted as the ratio of the probability of success (survival) over the probability of failure (mortality). For each top model, we used odds ratios as a measure of statistical significance of the association between each modelled traits and survival probability. Accordingly, all odds ratios were (>1 and <1) (Table 1), therefore the association between each modelled trait and survival probability was statistically significant (Figs 2–4). If we take leaf biomass as an example, we see that one unit increase in this predictor, led to a 9.7% and 9.9% increase in the odds of *I. carnea* survival in canal bank and wasteland respectively, assuming that other variables are fixed (see Table 2).

Discussion

In our study we showed that plant attributes associated with the survival of the invasive species *I. carnea* differed by urban habitat type. Confirming recent calls for the inclusion of intraspecific variation in ecological studies, we showed that growth and biomass allocation traits were indeed important for predicting species performance, but that the important traits differed among the habitats analyzed. Our results showed that using morphological plant traits provides a simple approach to understand invasive species survival in novel habitats. The critical conclusion is that while the measured traits did influence survival of *I. carnea*, the importance of specific traits was contingent on the local environment, meaning that local trait-environment interactions need to be understood in order to predict and plan for invasive species.

Our study showed a clear selection of traits in different habitats (Table 2, Figs 2–4). In canal banks habitat, the interaction among leaf biomass, root biomass, number of flowering ramets and non-flowering ramets has a significant effect on the survival rate of *I. carnea*. In waste lands, leaf biomass, root biomass, number of leaves and stem diameter, but in roadsides stem diameter, number of flowering ramets and non-flowering ramets. Consequently, growth and survival of this species was a function of measured traits, especially those reflecting size.

However, it should be noted that size-based traits were the best predictors for invader survival, which is in some ways not surprising. It is well known that larger plants have higher survival probabilities and greater reproduction (Horvitz and Schemske 2002). Larger plants are those individuals that have already experience successful growth and might reflect the fact that these individuals are in locations with

optimal micro environmental conditions. Yet, what was unexpected was that different size traits predict survival in different habitats.

Traits linked to invader colonization in new environments are those most likely to predict invasion success. Trait-environment relationships were also consistent with general patterns observed along large ecological gradients (Ozenda 1985, Pornon et al. 2007). In a meta-analysis of trait comparisons related to invasiveness, shoot allocation, leaf-area allocation, physiology, size, growth rate, and fitness were found to be most important for plant invader success (Van Kleunen et al. 2010).

From the top models, our study showed a significant relationship between leaf traits and different habitats. For example, there was a positive significant effect of the number of leaves on the survival probability of *I. carnea* in wastelands, whereas survival probability decreased significantly with increasing leaf biomass in canal banks and wastelands habitat. Moodley et al. (2013) stated that for some plant traits there are clear mechanisms for the association of selected traits and invasion success, also some traits show differing responses at the different stages of invasion. Leaf traits in particular have been linked to invader success, including a large meta-analysis of local and global leaf traits predicting invasion (Leishman et al. 2007). Leaf growth and production is dependent upon the rate of supply of limiting resources (Shinozaki and Kira 1956). Both leaf area and leaf consistency are related to the moisture conditions prevailing in the habitat occupied by the plant. The moisture conditions are reflected by climatic and soil factors and it may be difficult to distinguish between the effects of either (Werger and Ellenbroek 1978).

It should be noted that the three habitat types were spatially segregated and thus the analyses would be pseudo replicated if included in single statistical models (Hurlbert 1984). We analyzed the three habitats separately and our expectation was that if trait-performance relationships were robust enough, we should see similar patterns in the different habitats. Yet trait-performance relationships were quite different at the different sites. Future studies should find more habitat replicates or design experiments to delve deeper into the trait-environment relationships.

This study concluded that trait-environment interactions are critical predictors of invader species survival and subsequent success in novel urban habitats. As invasive plant species continue to pose significant threat to natural areas, understanding how they interact in novel, urban habitats is often a first step to understand the dynamics of invasive species in more pristine and protected habitats. Our approach was able to predict the local abundance of *I. carnea* across a large ecological gradient. Also it can help to assess monitoring of invasive species in native Egyptian ecosystems. We gain a better insight on the rapid growth and adaptability of *I. carnea* from dry to aquatic habitats which may indicate that this plant is capable of rooting within a few days (Cook 1987, Chaudhuri et al. 1994, Shaltout et al. 2010). Due to the invasion of *I. carnea*, diversity of native Egyptian wetland flora and fauna is being reduced (Eid 2002). By understanding which traits are correlated to invasion success of *I. carnea*, what the mechanisms behind such correlations are, and under which conditions invasions are favoured can provide accurate predictive tool to reduce the impact of invasive species.

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Supplementary material I**Table 1S. Comparison of stratified multivariable generalized linear models**

Authors: Reham F. El-Barougy, Marc W. Cadotte, Abdel-Hameed A. Khedr, Reham M. Nada, J. Scott MacIvor

Data type: PDF file

Explanation note: Comparison of stratified multivariable generalized linear models that model the relationship between survival probability and different variables. The best model, selected by AIC, p-value of chi square, deviance explained (DE) and (AW). AW is the Akaikes weight which is the probability of the model being the best model explaining the relationship between survival probability and different variables. DE is the percentage of deviance explained (DE) as a measure of the model's goodness-of-fit.

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